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Contents lists available at ScienceDirect

Pedobiologia - International Journal of Soil Biology

journal homepage: www.elsevier.de/pedobi

Relationships among spatial distribution of soil microarthropods, earthworm species and soil properties

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ARTICLE INFO

Article history:

Received 22 February 2010

Received in revised form 9 July 2010

Accepted 9 July 2010

Keywords:

Microarthropods

Earthworms

Spatial distribution

Geostatistics

Edaphic factors

Interspecific relationships

ABSTRACT

This paper examines the spatial distribution pattern of earthworm species and microarthropod groups, with the aim of detecting and explaining the relationships between them. Microarthropods and earthworms were sampled at 42 uniformly distributed points, with physical and chemical analyses performed at each site as well. Distribution patterns were described using geostatistical tools. Aggregation of populations, determined using a dispersion index, showed that all soil groups presented clumped distributions. Geostatistical analysis indicated that soil groups were spatially auto-correlated and facilitated a description of the spatial pattern of each group. Cross-semivariograms showed cross-correlation of different types (either negative or positive) between various groups of microarthropods and some earthworm species. Mantel tests were used to assess these correlations and to determine whether the relationships were true or spurious. Partial Mantel tests confirmed positive relationships between *H. elisae* – Isotomidae and *A. trapezoides* – Entomobryidae and negative relationships between *H. elisae* – Poduromorpha, *H. elisae* – other arthropods and *A. rosea* – Gamasida. No true relationships were found between fauna distribution and soil physical/chemical properties. Different earthworm species influenced each microarthropod group in diverse ways showing complex relationships between them. Additional manipulative experiments are necessary to unravel the processes affecting the specific patterns observed in the present study.

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Introduction

From an ecological perspective, soil represents an interactive system consisting of different components: the soil's physical and chemical characteristics, organic matter and biological activities (Coleman et al. 1992). Microarthropods and earthworms are two of the main groups of organisms found in soil systems. They take part in the biogeochemical cycles of the soil and affect its biological fertility by decomposing organic materials, nutrient recycling and stimulation of fungal and bacterial metabolism (Lebrun 1979; Brown 1995).

Two species may exhibit dissimilar distributions if they have different responses to environmental conditions or if they have negative interspecific relationships (Jiménez and Rossi 2006). The relative importance of biotic and abiotic factors that modify organization of communities has received considerable attention in the ecological literature. Important abiotic factors determining soil fauna composition include vegetation type, soil structure, soil chemistry, organic matter, soil microflora and soil moisture and

temperature (Butcher et al. 1971; Wallwork 1971; Adejuyigbe et al. 1999; Hasegawa 2001; Margerie et al. 2001; Coulson et al. 2003; Hernández et al. 2003; Sousa et al. 2003; Blackshaw et al. 2007). Interspecific relationships can also determine the spatial distribution of soil fauna. Some authors have considered predator relationships as a factor determining the distribution of fauna, especially among arthropod groups (Bonte and Mertens 2003; Warner et al. 2003). Soil fauna groups can also compete for food resources, because most of them feed on higher plants, pollen, microflora, algae, certain dark pigmented fungi and detritus or dead organic matter (Mitchell and Parkinson 1976; Maraun et al. 1998). Saprophagous microarthropods have a feeding behaviour similar to that of earthworms, and competition between these groups has been postulated by several authors (Dunger 1991; McLean and Parkinson 1998; Scheu et al. 1999; Migge 2001; Gutiérrez et al. 2008). The spatial pattern of soil biota is controlled by biotic and abiotic conditions, but some species, like ecosystem engineers, may dramatically affect the physical structure of their habitat, potentially affecting the distribution of other species. In this way, earthworms act as “ecosystem engineers”, modifying the physical, chemical and biological properties of the soil via the production of casts and galleries, influencing soil structure, carbon and nitrogen cycles and water regimes as well as the organisms that inhabit it –

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including microarthropods (Lee 1985; Lavelle 1988; Brown 1995; Edwards and Bohlen 1996; Lavelle and Spain 2001).

Earthworms could have some effect on the number and species richness of soil microarthropods as several authors have reported, both in a negative (Lagerlöf and Lofs-Holmin 1987; Scheu and Parkinson 1994; McLean and Parkinson 1998; Scheu et al. 1999; Maraun et al. 2001; Migge 2001; Gutiérrez et al. 2003) or a positive way (Marinissen and Bok 1988; Wickenbrock and Heisler 1997; Loranger et al. 1998; Salmon and Ponge 1999, 2001; Schrader and Seibel 2001; Tiunov 2003; Salmon et al. 2005). The effect of earthworms on microarthropods could be variable depending on their taxonomic groups, the season or the type of habitat and vegetation (Hamilton and Silman 1989; Maraun et al. 1999; McLean and Parkinson 2000). Most of the field studies on earthworms have focused on species belonging to the genus *Lumbricus*, which are anecic, feed on superficial organic matter and build vertical galleries. Very few field studies have looked into the relationships between microarthropods and endogeic earthworms (e.g., Loranger et al. 1998; Migge 2001) such as the Homogastridae, which are also responsible for pronounced changes in soil physical structure (Brown 1995). In the laboratory, clear negative effects of the endogeic earthworm *Hormogaster elisae* on the abundance and mobility of microarthropods were reported (Gutiérrez et al. 2003, 2009), indicating that this negative effect was not likely to be caused by the active predation of the microarthropods by earthworms (Gutiérrez et al. 2006), but rather a possible competition relationship between both groups (Gutiérrez et al. 2008). Other authors (Marinissen and Bok 1988; Hamilton and Silman 1989; Loranger et al. 1998; Maraun et al. 1999; Schrader and Seibel 2001; Tiunov 2003) have previously sampled microarthropods in middens or burrows of anecic species but regular simultaneous grid sampling of microarthropods and earthworms in a relatively large plot has never been done before.

Autocorrelation is a potential problem in many field samplings; samples are not independent because the samples collected closer to each other are often more similar among them than the ones collected farther away. Soil living organisms are rarely spatially independent at a field scale of <100 m (Robertson 1987). For example, earthworms have characteristic spatial patterns at scales ranging from 1 to 50 m (Rossi et al. 1995; Decaëns et al. 2009) and mites have shown a patch size from 20 cm to a few metres (Klironomos et al. 1999). When autocorrelation is present among data, conventional statistics are no longer valid and specific statistical analyses are required to distinguish between true and false relations. Conventional methods basically separate three types of distributions (random, regular and aggregated), giving a quantitative measurement of the amount of aggregation, but not of the true spatial pattern (Rossi et al. 1996). Geostatistics is a useful method to determine the spatial structure of soil organisms and their degree of autocorrelation. This method allows the analyses of the complex relationships between biological and environmental variables (Rossi et al. 1995) and has been applied in previous studies of soil ecology and distribution of earthworms and microarthropods (Rossi et al. 1996, 1997; Cannavacciuolo et al. 1998; Rossi and Quénehervé 1998; Klironomos et al. 1999; Decaëns and Rossi 2001; Jiménez et al. 2001; Rossi and Nuutinen 2004; Barot et al. 2007; Hernández et al. 2007; Decaëns et al. 2009).

The aim of the present work is to describe the spatial pattern of microarthropod and earthworm communities in an experimental plot at El Molar (Madrid, Spain) using geostatistical methods in addition to conventional approaches based on aggregation indexes. By examining the spatial distributions of these two soil groups, the study also attempts to determine the relationships between them and with soil parameters and whether the negative effect of *H. elisae* on microarthropods observed in the laboratory occurs in the field.

Materials and methods

A sampling survey was undertaken at El Molar, 42 km to the northeast of Madrid (U.T.M.30TVL525095; altitude 817 m). The site is situated within the transitional area between the mountains of Central System of Spain and the plateau to the south. The climate of the area is temperate Mediterranean but suffers from extreme conditions due to its latitude with mild, rainy winters and long, hot, dry summers (Da Gama et al. 2003). Only subnitrophilous pasture and a few woody, aromatic plants are found in the plot. The climatic and edaphic characteristics of the site are fully described in Valle et al. (1997) and Gutiérrez et al. (2006).

The dimensions of the experimental plot were 112 m × 84 m. It was divided into 42 squares of 16 m × 14 m. Soil samples were taken from the top right-hand region of each square. Square soil samples (25 cm × 25 cm × 10 cm) were collected for the extraction of microarthropods in the laboratory; these were removed from aliquots of 400 g of the homogenized soil following the Berlese–Tullgren method (Krantz 1978). Extraction from a defined weight of soil was performed following the methodology of Maraun et al. (1999) and Tiunov (2003). The extracted microarthropods were preserved in Scheerpeltz solution, identified and enumerated. Earthworms were extracted using formalin and hand sorting from soil samples (100 cm × 50 cm × 25 cm) located to the right from where the microarthropods samples were taken. The earthworms were fixed in a solution of 1:1 10% formalin and 96% ethanol for several minutes and stored in glass tubes in 10% formalin until identification.

Soil parameters were analysed as follows. In order to collect samples for the determination of soil structure (moisture content, aeration and porosity), a soil core (cylinder of known weight and volume) was introduced into the soil just to the right of the place where earthworm samples were extracted. These variables were determined as indicated by Guitián and Carballas (1976). Vegetation-free soil samples weighing approximately 500 g were taken from an area close to where the core was introduced for the determination of other soil physical and chemical soil properties. Samples were air-dried and sieved to 2 mm and soil texture was determined as indicated by Guitián and Carballas (1976). The total percentage of organic carbon (%C) was determined using the method of Anne (1945) and that of nitrogen (%N) by the Kjeldahl method, as described by Page et al. (1982). The C/N ratio and the percentage organic matter were then calculated.

Different types of dispersion coefficients (ID: Index of Dispersion; ICS: Index of Cluster Size; I_M : Morisita's Index) were calculated to determine the type of spatial distribution of each taxa (Huflejt and Karwowski 1993). Moran's I coefficient was used to measure the autocorrelation between factorial coordinates on the first axis of a Principal Components Analysis made with the values of microarthropods, earthworms and soil parameters. The overall significance was tested with the Bonferroni method of correction for multiple comparisons (Rossi and Quénehervé 1998). Geostatistical methods were used to determine the spatial distribution of soil organisms. Semivariance, $\gamma(h)$, was calculated following the expression used in Robertson (1987), Rossi et al. (1995) and Hernández et al. (2007). A semivariogram was used to express the relationship between semivariance of a variable and separation among samples, and it was adjusted to different theoretical models to describe the degree of spatial dependence of the variable. We must consider that the semivariogram shows only a slight spatial structure and it is very difficult to fit a good semivariogram model (Einax and Soldt 1999). As McBratney and Webster (1983) showed, the goodness of fit of a semivariogram model is a function of the number of samples, and a small number of samples could cause a small number of semivariogram points, a bad fit of the semivariogram model, and consequently a large estimation variance.

Nugget effect occurs when $\gamma(0) > 0$ caused by sampling errors or by the spatial variability occurring within the minimum distance interval (no spatial structure is detected, data are randomly distributed and not autocorrelated at the scale used in the sampling design). Once spatial dependency was established, semivariograms were used to interpolate values for points not measured using kriging algorithms.

The relationship between microarthropod and earthworm abundance was examined by cross-semivariogram analysis to find possible spatial correlations between group distributions (Rossi et al. 1995). To examine relationships between soil fauna and physical and chemical properties of the soil, cross-semivariograms were also made between soil groups' abundance and the values on the first axis of the PCA made with soil parameters. Finally, simple and partial Mantel tests (Mantel 1967) were used to assess the links between the spatial patterns of earthworm species and microarthropod groups and between spatial patterns of soil groups and soil parameters. Three types of distance matrices were used: (1) species or taxonomic groups distance matrices were formed by taking the differences among the values of abundances for all possible pairs of sampling locations, (2) a soil parameters distance matrix was formed by taking the differences among the values in the first axis of the PCA for all pairs of sampling locations, and (3) finally a geographic distance matrix was formed calculating the Euclidean distances between every pair of sampling locations. Simple Mantel tests measure the extent to which the variation in one matrix corresponds to that in a second and were first performed to determine whether the correlations observed with the cross-semivariograms were true or spurious. When simple Mantel test results were significant, partial Mantel tests were performed computing a partial correlation between two matrices while controlling for the geographic distance matrix to test whether the apparent relationship between two variables was spurious or not (Rossi and Quénéhervé 1998; Valckx et al. 2009). Partial Mantel tests, however, are not always easy to interpret due to complicated permutation strategies applied in order to derive a significance test (Legendre & Legendre 1998). Semivariograms, Kriged maps and cross-semivariograms were performed using GS+v.9 (Geostatistics for the Environmental Science) Gamma Design Software (www.gammadesign.com). Mantel tests and Moran's correlograms were carried out with the statistical package "PASSaGE 2" (www.passagesoftware.net).

Results

Description of soil parameters

The soil of the plot was a heterogeneous sandy-clayey loam and soil parameters are shown in Table 1. Parameters of the models

Table 1

Means and standard errors (SE) for soil physical and chemical soil variables ($n = 42$ samples, except for % total sand, silt and clay where $n = 41$; data not available for sample 37).

Soil factors	Mean	SE
% Particles >2mm	35.18	6.05
% Total sand	66.33	8.83
% Total silt	13.33	4.98
% Clay	20.32	4.41
% Moisture	16.96	5.30
% Porosity	47.90	12.24
% Aeration	30.93	12.56
% Carbon	1.79	0.50
% Organic matter	3.09	0.87
% Nitrogen	0.15	0.04
C/N ratio	11.80	1.26
pH (H ₂ O)	6.6	0.5

to which the semivariograms of soil variables adjust to and kriged maps for these parameters are shown in Hernández et al. (2007).

Identification and distribution of the soil fauna

The earthworm species identified were *H. elisae* Álvarez, 1977 (Hormogastridae), *Allolobophora rosea bimastoides* (Cognetti, 1901), *Aporrectodea trapezoides* (Dugès, 1828) and *Octodrilus complanatus* (Dugès, 1828) (all belonging to Lumbricidae), and *Microscolex dubius* (Fletcher, 1887) and *Microscolex phosphoreus* (Dugès, 1837) (Acanthodrilidae). All species showed aggregated distributions, as suggested by their dispersion coefficients, all of which were >1 (Table 2). *Hormogaster elisae* was the most abundant earthworm followed by *A. rosea* and *A. trapezoides*. The geostatistical analyses revealed the existence of a spherical model for all three species and showed how these species are distributed in patches of a variable size. *Hormogaster elisae* is aggregated in patches of more than 50 m, while *A. rosea* is aggregated in patches of 17 m and *A. trapezoides* in patches of 30 m. Other earthworm species were occasionally found, but given their very small numbers, they were not included in the geostatistical analysis.

Both the collembolans and mite groups showed aggregated distributions; their dispersion coefficients were >1 (Table 2). Five groups of collembolans were identified (Poduromorpha, Isotomidae, Onychiuridae and Sminthuridae) and all four soil mite suborders (Gamasida, Acaridida, Actinedida and Oribatida) were represented. Collembolans were found to form patches from 20 to 27 m, except for Entomobryidae, which formed patches of 133 m. Spatial dependence was observed for all Collembolan groups, revealing a spherical or exponential model, except for Sminthuridae, for which a nugget effect was observed. The gamasid and acaridid mites showed spatial dependence with a spherical and exponential model, and formed patches of 17 and 30 m, respectively, while the members of Actinedida showed a dispersed distribution and a nugget effect. Within the Oribatida, representatives of Oribatida Macropylina and Oribatida Brachypylyna were recorded, as well as representatives of Poronota and Gymnonota. The members of Oribatida Macropylyna and Oribatida Gymnonota showed a nugget effect while the members of Oribatida Poronota indicated a spatial dependence with a spherical model and forming patches of 23 m. The remaining arthropods presented a nugget effect.

The proportion of the total model variance attributable to spatial structure ($C/C + C_0$) ranged from 0.00 (showing nugget effect for Sminthuridae, Actinedida and all Oribatida groups except for Poronota) but was high for nearly all groups, reaching values of 1.00.

Correlograms computed for the factorial coordinates of the PCA based on soil parameters and earthworm species showed significant autocorrelation. The pattern of these two Moran's correlograms were globally significant ($P = 0.02613$ for earthworms and $P = 0.00002$ for soil parameters) but suggested the presence of a gradient, the first autocorrelation values being positive and significant for the first classes of distances (28 m) with later values being negative and significant for the latter classes of distances (from 60 to 100 m). The microarthropods did not reflect a clear spatial structure, but small patches of positive or negative coefficients were observed for several distance classes. This observation might be attributed to the different levels of autocorrelation of each group, as was observed with the geostatistical analyses.

Relationships between different soil fauna groups

Cross-semivariograms revealed clear relationships between earthworm species and some microarthropod groups. Cross-semivariance values and the slope of the cross-semivariograms

Table 2
Means, standard deviations (SD), variances, dispersion coefficients and variogram model parameters for the abundance of groups of microarthropods and earthworm species (n=42 samples). Values for earthworms refer to 1 m × 0.5 m × 20 cm soil samples, those for microarthropods refer to 400 g of soil. ID: Index of Dispersion (* results of the χ^2 test with n-1 degrees of freedom); ICS: Index of Cluster Size; I_M : Morisita's Index.

Taxonomic group	Mean	SD	Variance	ID ($P=0.000^*$)	ICS	I_M	Variogram model type	Nugget variance (C_0)	Structural variance sill ($C_0 + C$)	Range (A)	r^2	Proportion ($C/(C_0 + C)$)
Total earthworms	6.33	8.08	65.30	10.318	9.318	2.442	Exponential	25.60	90.33	48.30	1.00	0.72
<i>H. elisae</i>	4.29	6.97	48.58	11.328	10.328	3.365	Spherical	19.20	73.24	51.30	1.00	0.74
<i>A. trapezoides</i>	0.52	2.02	4.08	7.752	6.752	14.182	Spherical	0.25	4.05	30.10	1.00	0.94
<i>A. rosea</i>	1.07	3.45	11.90	11.081	10.181	10.394	Spherical	0.01	8.68	17.80	0.00	1.00
<i>M. dubius</i>	0.04	0.31	0.10	2.500			-	-	-	-	-	-
<i>M. phosphoreus</i>	0.04	0.31	0.10	2.500			-	-	-	-	-	-
<i>O. complanatus</i>	0.35	2.31	5.36	15.314			-	-	-	-	-	-
Total Collembola	469.07	645.24	416334.66	887.568	886.568	2.845	Exponential	1000.00	399600.00	27.60	1.00	1.00
Isotomidae	151.31	155.87	24295.45	160.573	159.573	2.029	Exponential	3360.00	26540.00	21.90	0.45	0.87
Poduromorpha	307.38	552.21	304935.88	992.044	991.044	4.148	Spherical	11000.00	293600.00	25.50	1.00	0.96
Onychiuridae	6.14	9.21	84.82	13.814	12.814	3.044	Spherical	5.40	90.17	21.50	0.51	0.94
Entomobryidae	2.78	12.37	153.01	54.888	53.888	20.047	Gaussian	108.10	359.90	133.89	0.98	0.69
Sminthuridae	1.45	1.94	3.76	2.593	1.593	2.088	Linear	3.66	3.66	48.05	0.17	0.00
Total Acari	79.73	50.48	2548.23	31.952	30.952	1.379	Linear	2753.41	2753.41	48.05	0.00	0.00
Gamasida	19.76	14.38	206.78	10.458	9.458	1.468	Spherical	6.90	213.60	17.80	0.00	0.97
Acaridida	4.69	7.38	54.46	11.601	10.601	3.217	Exponential	4.10	56.51	30.30	0.90	0.93
Actinedida	20.59	22.13	489.73	23.787	22.787	2.081	Linear	568.47	568471.00	48.05	0.90	0.00
Oribatida	34.69	26.92	724.68	20.896	19.896	1.560	Linear	716.72	716.72	48.05	0.81	0.00
Macropylina	4.26	9.54	91.01	21.358	20.358	5.689	Linear	104.69	104.69	48.05	0.00	0.00
Gymnonota	5.23	11.69	136.65	26.111	25.111	5.701	Linear	105.74	105.74	48.05	0.13	0.00
Poronota	25.14	22.65	513.02	20.411	19.411	1.754	Spherical	11.00	452.90	23.40	0.92	0.98
Other arthropods	10.73	14.07	197.96	18.443	17.443	2.589	Linear	164.77	164.77	48.05	0.24	0.00

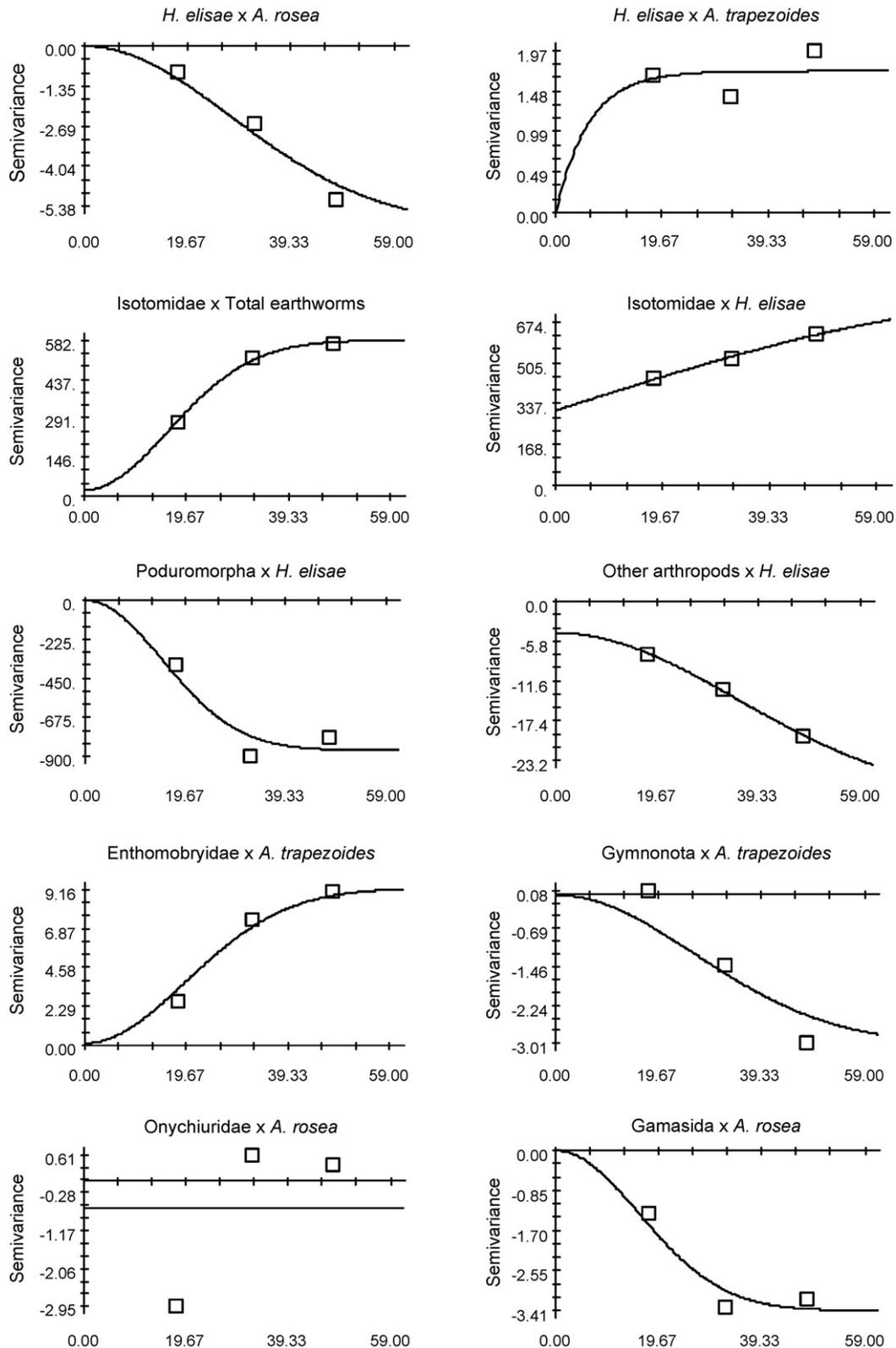


Fig. 1. Cross-semivariograms performed between some taxonomic soil groups. Abscissa: separation distance (m).

were variable, positive or negative, depending on the taxonomic group, revealing consistent positive or negative relationships. Fig. 1 shows the most characteristic relationships. Regarding the earthworm species, *H. elisae* showed a positive relationship with *A. trapezoides* but a negative one with *A. rosea*. When species of earthworms and microarthropod groups were compared, we found *H.*

elisae to have a consistent positive relationship with Isotomidae, Gamasida, Macropylina and Poronota and a negative relationship with Poduromorpha, Onychiuridae, Entomobryidae, Sminthuridae, Gymnonota and other arthropods. *Aporrectodea trapezoides* presented positive relationships with Isotomidae, Entomobryidae, Sminthuridae and Gamasida and negative ones with Onychiuridae,

Table 3
Results of simple and partial Mantel tests between two matrices M1 and M2. In all cases a partial Mantel test was performed to check for those relationships while correcting for a third matrix called space (geographic distances among sampling points). Significant differences are marked with an asterisk. M2: Ph-Ch: soil parameters distance matrix formed by taking the differences among the values in the first axis of the PCA for all pairs of sampling locations.

Matrix	Simple Mantel test			Partial Mantel test		
	Correlation	<i>t</i>	<i>P</i>	Correlation	<i>t</i>	<i>P</i>
M1: Total earthworms M2: Isotomidae	0.257	2.291	0.010*	0.256	2.290	0.011*
M1: <i>H. elisae</i> M2: Isotomidae	0.299	2.597	0.004*	0.298	2.604	0.004*
M1: <i>H. elisae</i> M2: Poduromorpha	-0.112	-0.868	0.001*	-0.111	-0.871	0.010*
M1: <i>H. elisae</i> M2: Other arthropods	-0.111	-0.868	0.024*	-0.107	-0.845	0.038*
M1: <i>A. trapezoides</i> M2: Entomobryidae	0.246	1.607	0.036*	0.246	1.606	0.039*
M1: <i>A. trapezoides</i> M2: Gymnionota	-0.068	-0.453	0.011*	-0.066	-0.442	0.090
M1: <i>A. rosea</i> M2: Onychiuridae	-0.087	-0.629	0.043*	-0.087	-0.629	0.063
M1: <i>A. rosea</i> M2: Gamasida	-0.110	-0.849	0.003*	-0.107	-0.834	0.012*
M1: Isotomidae M2: Ph-Ch	-0.050	-1.702	0.044*	-0.035	-0.360	0.359
M1: Gymnionota M2: Ph-Ch	0.038	-1.787	0.036*	0.038	0.343	0.634
M1: Poronota M2: Ph-Ch	-0.008	-2.141	0.016*	-0.018	-0.233	0.407

Actinedida, Acaridida and Gymnionota. Finally, *A. rosea* indicated few consistent relationships, being positively related to Acaridida and Gymnionota and negatively to Gamasida, Actinedida and Macropyliina.

Simple Mantel statistics (Table 3) indicated the presence of a consistent spatial pattern only for few of the relationships found using the cross-semivariogram analyses. The partial Mantel test (used to check for those relationships while correcting for space) was significant and positive for the relationships between *H. elisae* and Isotomidae and between *A. trapezoides* and Entomobryidae while it was significant but negative for the relationships between *H. elisae* and Poduromorpha, *H. elisae* and other arthropods and *A. rosea* and Gamasida. This means that the similarity observed between the spatial patterns of organization of these pairs of soil groups corresponded to a true correlation. Partial Mantel statistics were not significant for the relationships between *A. trapezoides* and Gymnionota, and between *A. rosea* and Onychiuridae that were previously significant with the simple Mantel test, indicating the absence of a true relationship between these matrices when the test is run by holding space constant. These last relationships were thus simply due to spatial patterns leading to a spurious correlation.

Relationships between soil fauna groups and soil parameters

The cross-semivariogram analysis (Fig. 2) revealed clear positive relationships of Isotomidae, Sminthuridae, Actinedida and Macropyliina, with high values of pH, clay, % total silt, % carbon, % nitrogen, % organic matter and soil moisture. On the other hand, *H. elisae*, *A. trapezoides*, Poduromorpha, Entomobryidae, Acaridida, Gymnionota and Poronota, were associated with high values of % total sand, porosity, aeration and C/N ratio. However, the partial Mantel test indicated the absence of consistent spatial patterns for all these relationships; none of these tests were significant when run while holding a space constant, indicating that the patterns were simply due to spatial patterns and not to a true correlation.

Discussion

There is much debate on the factors influencing the distribution of soil organisms. Physical/chemical, climatological and geomorphological factors are often those that most heavily influence plant and animal distributions, but interspecific relationships, such as competition, predation or processes related to growth and development, are also important (Boccard et al. 1992). All the soil groups investigated in this study showed aggregated distributions, the most commonly observed distribution for soil organisms, which are generally due to environmental heterogeneity, social cooper-

ation, gregariousness and other factors (Wallwork 1976; Huflejt and Karwowski 1993). The results from the geostatistical analyses have shown that most of the soil fauna groups are significantly autocorrelated and reflect a clear spatial structure. Earthworms were aggregated in patches from 17 to more than 50 m and most of microarthropod groups in patches from 17 to 30 m. These findings correspond to results of previous studies where soil organisms were observed to be highly aggregated in hot spots and structured at various spatial scales – usually one of only a few tens of metres (Klironomos et al. 1999; Decaëns and Rossi 2001).

The horizontal distribution of soil organisms is complex and structured at different spatial scales (Rossi 2003a,b,c). Ecological processes could have different patterns at each spatial scale, as they are controlled by several mechanisms (García 2006) and differ for diverse ecological systems and questions (Wiens 1989). Several studies outline the importance of multi-scale approaches for spatial analysis (Birkhofer et al. 2006; Gießelmann et al. 2007); this is an important aspect that only recently has received considerable attention. In the present study, the same spatial scale was used for all the variables; anyway, spatial statistics offers the possibility of evaluating the spatial structure of a variable in several scales by means of correlograms and semivariograms. Cross-semivariograms allowed definition of the scales with high levels of autocorrelation for two variables. In any case, the possibility of not having detected some patterns between different variables in the present study must be considered, as they may have occurred at different spatial scales.

Several factors could influence soil fauna distribution at the plot in El Molar. The partial Mantel test indicated non-significant relationships between soil parameters and the abundance of any soil fauna group (neither the earthworms nor the microarthropods). This is surprising since abiotic factors usually have great influence on the distribution of most soil animals. *Hormogaster elisae* and *A. trapezoides* were previously found to be positively correlated with soil porosity, aeration and sand, and *A. rosea* with high values of clay and organic matter in the same experimental plot (Hernández et al. 2003). In Mediterranean regions, water content seems to be the most important factor (followed by temperature) determining the habitat of Collembola and Acari (Arbea and Blasco-Zumeta 2001), but Hernández et al. (2007) found similar conditions of water content for all their samples and the temperature variation would have been low, as the plot was a meadow with neither tree vegetation nor sunny/shadow places. Similarly, Hasegawa (2001) found no clear correlation between the total abundance of Collembola and Oribatida and total organic matter. It should also be noted that the partial Mantel test could be difficult to interpret (Legendre and Legendre 1998) and that a non-significant result is not always an indication for the absence of a biological effect.

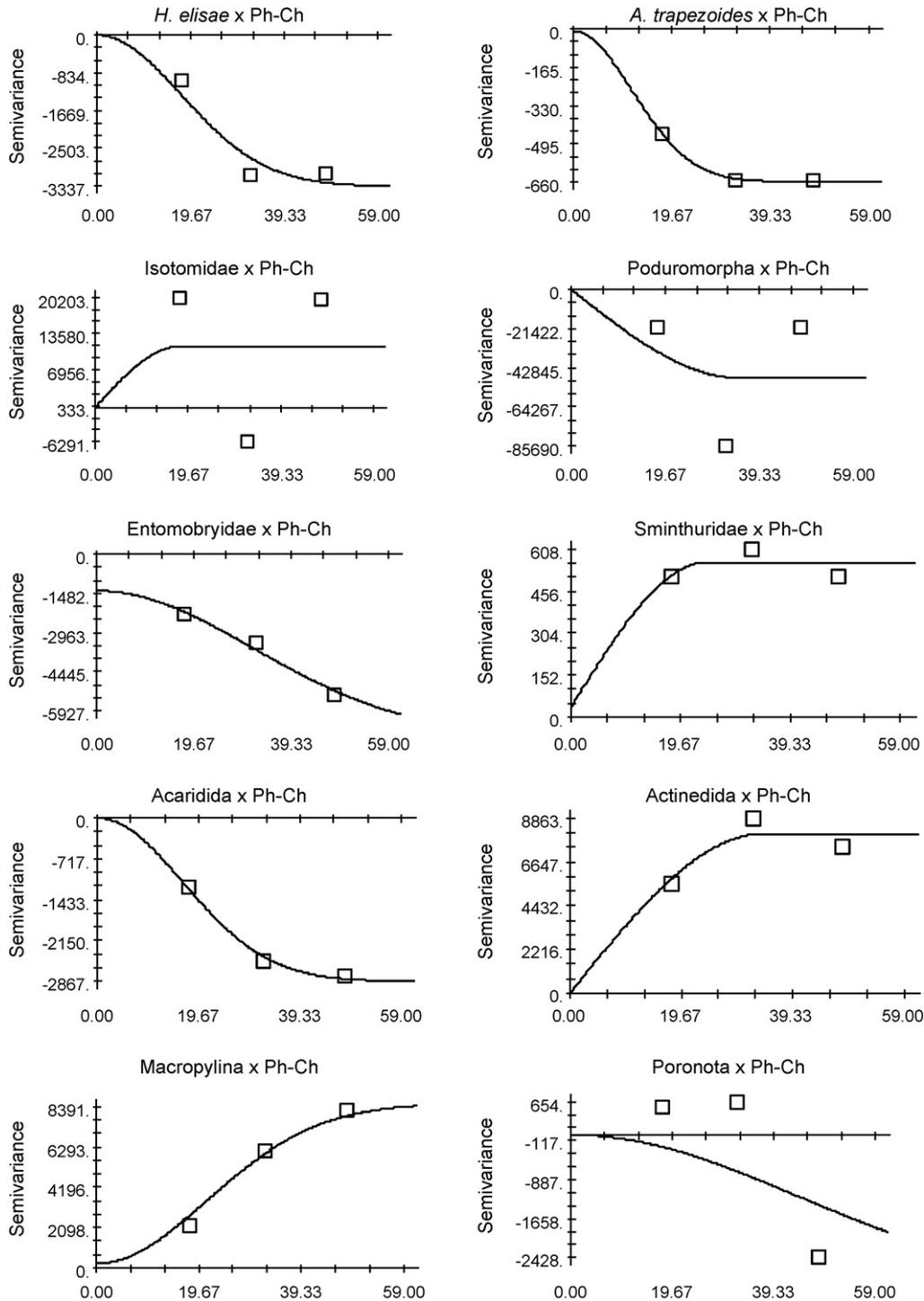


Fig. 2. Cross-semivariograms performed between some taxonomic soil groups and soil parameters. Abscissa: separation distance (m).

With respect to the relationships between earthworm species and microarthropod groups, results of the cross-semivariogram analysis and Mantel tests revealed only a few clear relationships, either positive or negative depending on the taxonomic group. The most abundant earthworm species *H. elisae* showed a consistent negative relationship with the most abundant microarthropod group, the Poduromorpha, and with other arthropods. The earthworm *A. rosea* also showed a negative relationship with Gamasida. These relationships could have determined the tendency of the microarthropod community when studied globally in other anal-

yses and experiments, and suggest that the negative relationship observed in the laboratory between microarthropods and *H. elisae* (Gutiérrez et al. 2003) may also exist in the field but only with some taxonomic groups and probably only with a few species. However, positive relationships were also observed between the earthworm species *H. elisae* and *A. trapezoides* and the Isotomidae and Entomobryidae, respectively.

The relationships between earthworm species and microarthropod groups found in this study could be due to different reasons. Some groups or species of microarthropods may compete with

earthworms for the same food resources (Wallwork 1971; Brown 1995; Gutiérrez et al. 2008) as earthworms are detritivorous, fungivorous and microbivorous. Predatory microarthropods (such as Gamasida mites) might be indirectly affected by the greater abundance of prey (e.g., collembolans Poduromorpha). A trophic interaction would also explain positive relationships with some other groups; some collembolans (such as the Isotomidae) would be attracted to the earthworm excreta and use them as food resource, as observed by Salmon and Ponge (1999, 2001). Earthworms may affect the structure and functioning of the soil via their casts and galleries, as well as by taking an active part in energy and nutrient cycling (Lee 1985; Lavelle 1988; Brown 1995; Edwards and Bohlen 1996). In terms of this latter role, it is important to distinguish between the positive effects of the earthworm burrows, which microarthropods can use to increase their living space and escape from predators (Salmon et al. 2005), and the negative burrowing activity of earthworms, that may homogenize the soil environment and provoke soil perturbation (Marinissen and Bok 1988; Loranger et al. 1998; McLean and Parkinson 1998). Members of Oribatida, a particularly sensitive group of Acari, are especially likely to avoid such perturbation associated with earthworms (Norton and Palmer 1991), although this specific relationship was not clearly observed in the present study.

It is also important to separate the different effects of each species and ecological categories of earthworm on soil processes. While anecic species may have a positive effect on the density and diversity of soil microarthropods by forming vertical burrows, incorporating litter from the soil surface into deeper soil layers and transporting mineral soil materials to the surface by casting, endogeic species might have a negative effect on soil microarthropods by mixing organic and mineral soil materials, consuming the organic matter in mineral soil, and compacting the soil (Eisenhauer et al. 2007). In this study we found two endogeic earthworms, *A. rosea* and *H. elisae*; *A. trapezoides* seemed to be variable in its behaviour, similar to *Nicodrilus caliginosus meridionales* (Bouché 1972), being basically anecic but with some endoanecic (or even endogeic) populations (Fernández et al. 2010). The effect of these three earthworm species could have produced pronounced changes in the physical structure of the soil, which may have affected the abundance of soil microarthropods in different ways.

In conclusion, relationships between earthworms and microarthropods seem to be much more complex than expected. A confluence of multiple interacting processes probably affects the different distributions of soil groups and their relationships. Different earthworm species could likely influence each microarthropod species in diverse ways; this fact emphasizes the importance of undertaking ecological studies at the species level. However, spatial analyses from this study only provide information about spatial patterns at one point in time and at a specific scale, and only the correlations in spatial distribution of these groups have been shown. These correlations can arise from the influence of earthworms on microarthropods but additional manipulative experiments need to be performed to fully understand the processes affecting the specific patterns observed in the present study.

Acknowledgements

We wish to thank Dr. S. Migge-Kleian from Georg-August-University Göttingen and Dr. M.E. Mínguez from Universidad Complutense de Madrid for assistance with the identification of most groups of Acari found in this study and Dr. M.D. Jiménez and Dr. J.A. Delgado who kindly helped us with the interpretation of spatial statistic analysis. We also thank two anonymous reviewers for constructive suggestions that improved the manuscript.

Appendix A.

Species included in “Macropylina”: *Cryptacarus promecus* Grandjean, 1950; *Phyllozetes emmae* (Berlese, 1910); *Haplochthonius sanctaluciae* Grandjean, 1947; *Epilohmannia (cylindrica) cylindrica* Berlese, 1904.

Species included in “Brachypylina Poronota”: *Passalozetes africanus* Grandjean, 1932; *P. agricola* Mínguez y Subías, 1984; *Bipassalozetes reticulatus* (Mihelčič, 1957); *B. variatopictus* (Mihelčič, 1956); *Scutovertex granulatus* Mihelčič, 1957; *Galumna gibbula* Grandjean, 1956; *Pilogalumna alliferum* (Oudemans, 1919); *Peloptulus reticulatus* Mihelčič, 1957; *Minunthozetes reticulatus* Pérez-Íñigo, 1969; *M. quadriareatus* Mínguez, Subías y Ruiz, 1986; *Iugoribates cornutus* Mínguez, 1981; *Ceratozetes armatus* Mihelčič, 1956; *Zygoribatula cognata* (Oudemans, 1902); *Z. propinqua* (Oudemans, 1900); *Haplozetes sinuatus* Pérez-Íñigo Jr., 1990; *Schelorzetes labyrinthicus* Jeleva, 1962; *Hemileius robustus* Pérez-Íñigo, 1969.

Species included in “Brachypylina Gymnonota”: *Jacotella glabra* (Mihelčič, 1957); *Berlesezetes mirus* Mihelčič, 1956; *Tectocephus sarekensis* Trägårdh, 1910; *Quadroppia sp* Jacot, 1939; *Jobbopia dichosa* (Ruiz, Mínguez y Subías, 1988); *Discoppia (Cylindropia) cilindrica* (Pérez-Íñigo, 1965); *Medioppia media* (Mihelčič, 1956); *Medioppia subpectinata* (Oudemans, 1900); *Lauroppia sp* Subías y Mínguez, 1986; *L. similifallax* Subías y Mínguez, 1986; *L. baetica* Arillo y Subías, 1996; *Berniniella intrudens* Subías, Rodríguez y Mínguez, 1987; *Javieroppia cervus* Mínguez y Subías, 1986; *Multioppia (Multioppia) neglecta* Pérez-Íñigo, 1969; *Ramusella sp* Hammer, 1962; *R. (Ramusella) sengbushi* Hammer, 1968; *Ramusella (Rectoppia) mihelcici* (Pérez-Íñigo, 1965).

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